

Cultural Transmission and Evolution: A Quantitative Approach. By L. L. CAVALLI-SFORZA and M. W. FELDMAN. Princeton, N.J.: Princeton University Press, 1981. Pp. 328.

It is by now a commonplace that evolution by natural selection can be summed up in three Darwinian principles: (1) There is phenotypic variation among individuals (The Principle of Variation); (2) There is a correlation in phenotype between parents and offspring (The Principle of Inheritance); (3) Some phenotypes survive and leave offspring more than other phenotypes (The Principle of Selection). It is usually stated that these are necessary and sufficient conditions for evolution, since: if there is no variation, then there is nothing to select; if the variation is not heritable, then the selection will be ineffective in changing the population distribution in a cumulative way over generations; and if there is no selection, then the variation will be passed from generation to generation with no change in distribution.

What is not always realized is that these conditions are both less general and more general than they appear. In particular, there is no reason why the correlation between parents and offspring should be *genetic*. Any phenomenon that causes children to be phenotypically nonrandom with respect to their parents will do. Thus children may simply mimic their parents by learning, or they may catch their diseases: that is, "inheritance" may be nonbiological, or biological but nongenetic. This is the sense in which the three principles are more general than they are usually taken to be. However, the moment "heredity" is taken in this broader sense, quite new dynamics come into play. For example, cultural heredity can be negative, if children react against their parents by taking on an opposite phenotype, producing the so-called generation gap. Negative genetic correlations between parent and offspring are not usual, although, in fact, they do occur for sex-linked traits where sons resemble their mothers and daughters their fathers. More generally, nongenetic inheritance does not have the special property of unbiasedness that Mendelian segregation gives to heredity. Because heterozygotes produce a 1:1 ratio of the two types of gametes, then, in the absence of selection, no change in gene frequency occurs in large populations. It is the Mendelian ratio that makes the Hardy-Weinberg equilibrium work. But purely phenotypic transmission will not have this property, so the population may evolve simply as a consequence of the transmission rules themselves with no selection at all. There is, of course, a genetic equivalent to this asymmetry in the phenomenon of "segregation distortion" or "meiotic drive," which has the property of driving evolution of gene frequency, selection quite aside.

Cultural Transmission and Evolution is built on the realization that Mendelian transmission is a special case and explores the consequences of supposing characters to be transmitted by nongenetic routes. The reader should not be misled by the word "cultural" in the title. There is, indeed, a certain amount of discussion of "cultural" phenomena, but the authors are not committed to a particular theory of what culture is or how it changes. They ask, rather, the straightforward question: "What happens to the distribution of traits in populations when transmission is purely phenotypic?" The answer they give is: "It depends." In particular, it depends on what one supposes the transmission rules to be, on what the pattern of mating assortment is, and on whether the different phenotypes have different Darwinian fitnesses. In a sense, Cavalli-Sforza and Feldman have generalized all of elementary population genetics that are just special cases of the generalized transmission equations they derive. Moreover, they add to their models "mutations," that is, phenotypic innovations, and the effect of migration, finite population size, and population subdivision.

As the reader may guess, there are no strong general conclusions that can be reached from such phenotypic models, because the dynamics of the process are so dependent on the

details of transmission. The authors consider *vertical* transmission (parent to offspring, including adoptive parents since there are no genetics here), *oblique* transmission (across generation lines but from nonparents, including teachers), and *horizontal* transmission (within a generation). The method is simple and direct. All possible matings are tabulated phenotypically, and the distribution of phenotypes of the offspring are specified. These may then be modified by encounters with nonparents according to some frequency rule, and then weighted by Darwinian fitnesses. A recursion relation then is solved for both the dynamic and equilibrium properties of the model. Here, Marc Feldman, who is a master at investigating the properties of such dynamic systems, comes into his own, sucking out the complicated possibilities a maximum of useful results. The general features do not come as a great surprise to those used to population genetic models with meiotic drive and frequency dependence. Transmission alone drives the evolution of phenotype but can lead to fixation or equilibrium. Equilibrium also arises from the opposition of selection and transmission, and vertical transmission is more powerful than oblique or horizontal passage.

Inevitably, one comes to a comparison of *Cultural Transmission and Evolution* with another recent book on a similar topic, *Genes, Mind and Culture* by C. Lumsden and E. O. Wilson. The difference is best encapsulated in the observation that *Cultural Transmission and Evolution* is about *cultural inheritance* while *Genes, Mind and Culture* is about the *inheritance of culture*. Thus, Cavalli-Sforza and Feldman are able to make exact models of the phenotypic passage of individual traits without committing themselves to the absurd notion that culture is simply a collection of individual traits. Lumsden and Wilson, however, write about the genetic transmission of miscellaneous traits and then claim to have explained the origin of culture. Despite the fact that Cavalli-Sforza and Feldman do not add the complication of Mendelian inheritance to their models, they achieve such a richness of result as to defy any simple generalizations. How is it, then, that Lumsden and Wilson, with a much more complex model, are able to make general and powerful claims about the speed of cultural inheritance? The answer seems to be that, having a particular axe to grind, they have, in fact, carefully tailored their model to produce just the desired result. Unlike the disingenuous mathematizing of *Genes, Mind and Culture*, *Cultural Transmission and Evolution* is an open investigation of the properties of general models of phenotypic inheritance.

Alas, when Cavalli-Sforza and Feldman depart from the investigation of their models, even they occasionally slip into a carelessness about "culture." Thus, they speak of cars and language as "cultural objects" and of the dynamics of "cultural change" as somehow the dynamics of change in frequency of these "cultural objects." One has the impression that, despite their usual care not to take a simple reductionist view of culture and, indeed, their specific rejection of reductionism in their first chapter, there lurks somewhere in the background an equation of "cultural evolution" of traits with the "evolution of culture." Fortunately, these considerations do not affect the validity of their enterprise, which has opened up a new and rich field of theoretical investigation.

R. C. LEWONTIN

Harvard University
Boston

Neurofibromatosis (von Recklinghausen Disease). Genetics, Cell Biology, and Biochemistry. Advances in Neurology, vol. 29. Edited by V. M. RICCARDI and J. J. MULVIHILL. New York: Raven Press, 1981. Pp. 304. \$29.50.

"Neurofibromatosis seems to be a disease whose time has come," write John Mulvihill and Vincent Riccardi, the editors of this book on neurofibromatosis. In a way they are